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Spatiotemporal Impulse Response and Cortical Magnification

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According to a model of the spatiotemporal weighting function (Manahilov, V. Spatiotemporal visual response at suprathreshold stimuli. *Vision Research*, 1995, *35*, 227–237; and Triphasic temporal impulse responses and Mach bands in time. *Vision Research, 38*, 447–458) the waveform of the temporal-impulse response and the cortical spread of the spatial-impulse response should not depend on the retinal site of stimulation. To verify these model predictions, the spatiotemporal responses to brief near-threshold lines presented in the fovea and the near retinal periphery were studied. The effect of an inducing stimulus on the threshold for pattern detection of a test stimulus was measured, assuming that the pattern-detection threshold was determined by the test peak response. The spatial spread of the line response expressed in visual-field units was increased with eccentricity. The temporal-impulse responses to foveal and peripheral stimuli were similar. The model of the weighting function was used to evaluate the relative magnification factor for the retinal location tested. The calculated cortical spatial-impulse responses did not depend on the stimulation site. The data obtained are in line with the cortical magnification theory of peripheral vision.

Vision Impulse response Cortical magnification

INTRODUCTION

Recognition of visual objects is a primary function of vision. To understand the computational algorithms underlying object recognition, one should know how retinal images are represented in the visual network. Considering the visual system as a linear spatiotemporal filter, the response to any arbitrary stimulus may be specified by the weighting function of the system. The visual objects are mainly characterized by luminance distribution over space and time. The retinal images evoke neural activity occurring in time and space of the visual network. Thus, it is of interest to describe the image representation in both time and space.

Recently, the spatiotemporal responses to suprathreshold stimuli have been studied by a brightness matching technique (Manahilov, 1995, 1998). This approach is based on the assumption that the apparent brightness of a brief and spatially restricted test stimulus (line) is determined by the test peak response. The effect of inducing stimuli on the apparent brightness of the test line was employed as a measure of the spatiotemporal response to the inducing stimulus. It was found that the temporal-impulse responses to suprathreshold stimuli of small and large spatial dimensions consisted of three alternating phases, the middle one being the largest. This is in line with the established temporal analogue of the Mach bands at responses to temporal step stimuli. With this approach, the dynamics of the spatial spread of the response to a narrow bar was also studied. Initially, the spatial profile of the response was negative and was restricted in space, later the response was extended to adjacent positions achieving a triphasic form and still later it faded away.

These data were adequately described by a model of weighting function (Manahilov, 1995, 1998) which was approximated by a spatiotemporal Gabor-like function. The relative cortical magnification was involved in the expression of the weighting function as it is well known that the visual field is represented inhomogeneously in the visual cortex (Daniel & Whitteridge, 1961; Hubel & Wiesel, 1974). According to this model, the waveform of the temporal-impulse response as well as the cortical spread of the spatial-impulse response should not depend on the retinal site of stimulation. The present study was aimed at verifying these model predictions.

The above-mentioned data concern spatiotemporal responses to suprathreshold stimuli. The visual system behaves more linearly at near-threshold stimulation. In most studies of the temporal-impulse response (Ikeda, 1966; Rashbass, 1970; Watson & Nachmias, 1977; Burr & Morrone, 1993) and the line (point) response (Fiorentini, 1972; Limb & Rubinshtein, 1977) the threshold contrast for detection of impulse pairs was

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measured. At contrast detection, however, the spatial- and temporal-impulse responses cannot be obtained directly because of the probability summation over space and time (Wilson, 1980; Watson, 1982). To measure directly the spatiotemporal response to an impulse stimulus of near-threshold contrasts, the spatial profile and the temporal waveform of the response should be traced by a test stimulus. To this end, the threshold contrast of the test stimulus has to be determined by the peak of the test response.

In the present study, the spatial spread and the temporal waveform of the response to a brief, near-threshold inducing line were evaluated by measuring the inducing-stimulus effect on the threshold for pattern detection of a test line. The pattern-detection threshold of the test stimulus was determined as the minimal contrast at which the stimulus was seen as a clearly defined line of a given (positive or negative) polarity. The pattern detection of the test line was thought to be determined by the extreme of the test-stimulus response.

MODELS

The model for pattern detection was assumed to consist of: (i) a linear spatiotemporal filter; and (ii) a threshold device for pattern detection which acts as a peak-response detector.

In our previous studies, the weighting function of the linear spatiotemporal filter was approximated by a Gabor-like function (Manahilov, 1995, 1998). The visual network was regarded as built up by several well-ordered neural layers. The output level was assumed to be located in the visual cortex at a normal distance z from the input (retinal) level (Manahilov, 1995—Fig. 7). Cartesian coordinates were used in both retinal and cortical planes regarding the retinal surface and the cortical surface as planar surfaces. The weighting function was aimed at describing the visual impulse response in time and space coordinates and was presented as follows:

$$h(x,y,t) = \frac{\cos[2(\pi(t-\tau-r/v+\varphi)/T]}{r} \times \exp[-0.5((t-\tau-r/u)/\sigma)^2]\exp[-0.5(r/\gamma)], \quad (1)$$

where $r = [(x-mx')^2 + (y-my')^2 + z^2)]^{1/2}$ is the distance between a given input point (x', y') and a given output point (x, y) of the visual network; z is the normal distance between the input and output level of the visual network; m is the relative cortical magnification factor indicating the scale of mapping from the striate cortex on the retina; T is the time period of oscillations; v is the phase velocity which characterizes the phase propagation of the cosine function; $u = v/\{1-(\alpha/r)[1-\exp(-0.5(r/\alpha)^4)]\}$ is the group velocity which determines the amplitude propagation of the Gaussian function; τ is a time delay needed to locate the extremum of the weighting function on the origin of the stimulus onset asynchrony (SOA) axis; σ, α and γ are constants and φ is a starting phase of the cosine function.

In order to reflect the spatial inhomogeneity of the visual system (Daniel & Whitteridge, 1961; Hubel & Wiesel, 1974), the relative magnification factor m was incorporated in equation (1). Thus, the distance r between a given input point (x',y') and a given output point (x, y) of the visual network depends on the differences $x - mx'$ and $y - my'$.

Since the visual system is inhomogeneous in space, it is a space-variant system. However, for a given restricted retinal area, the relative cortical magnification factor may be regarded as a constant. In this case, the system may be considered space-invariant and the response $g(x, y, t)$ to a line stimulus in time and in space could be calculated as follows:

$$g(x,y,t) = C\int_{-a/2}^{a/2}\int_{-b/2}^{b/2}\int_0^{\Theta} h(x'-x, y'-y, t'-t)dx'dy'dt' = CG(x,y,t) \quad (2)$$

where: θ is the stimulus duration; a and b are the width and the length of the stimulus and C is the stimulus contrast.

The measurement of the spatiotemporal response to a brief line stimulus was based on: (i) the linear assumption, i.e., the visual system is characterized by additivity and homogeneity; and (ii) the peak-detection assumption, i.e., the stimulus is detected as a well-defined line of a given polarity when the extreme of the stimulus response reaches or exceeds a constant threshold level.

Let us consider the perturbation caused by a brief inducing line on the threshold contrast for pattern detection of a brief test line. The ratio between the contrast of the inducing stimulus (open bars) and the contrast of the test stimulus (dark bars) is zero (A), −0.25 (B), −0.50 (C) and −0.75 (D) (left graphs of Fig. 1). Both stimuli are one-dimensional spatial impulses (lines) with a short duration. They are presented at a given SOA (t_s) and at a given distance (δ). The imaginary impulse responses to the inducing stimulus (dotted line) and the test stimulus (thin line) are shown on the right graphs of Fig. 1. The thick lines denote the resulting response at the threshold level (K) for pattern detection of the test stimulus. Assuming that the responses to the test and the inducing stimulus are summed linearly as well as that at pattern detection the extreme of the test-stimulus response reaches a given threshold level, we could write:

$$C_0G_t(x_{extr}, 0, t_{extr}) = C_tG_t(x_{extr}, 0, t_{extr}) + C_iG_i(x_{extr}-\delta, 0, t_{extr}-t_s) \quad (3)$$

where: C_0G_t $(x_{extr}, 0, t_{extr})$ is the extreme value of the response to the test stimulus at pattern-detection threshold in the absence of the inducing stimulus; C_tG_t $(x_{extr}, 0, t_{extr})$ is the extreme value of the test response in the presence of the inducing stimulus; and C_iG_i $(x_{extr}-\delta, 0, t_{extr}-t_s)$ is the value of the response to the inducing stimulus at moment $t_{extr}-t_s$ and space coordinate $x_{extr}-\delta$.

Because equation (3) refers to vertical lines parallel to the y-axis, for simplicity the space coordinate (y) is set to

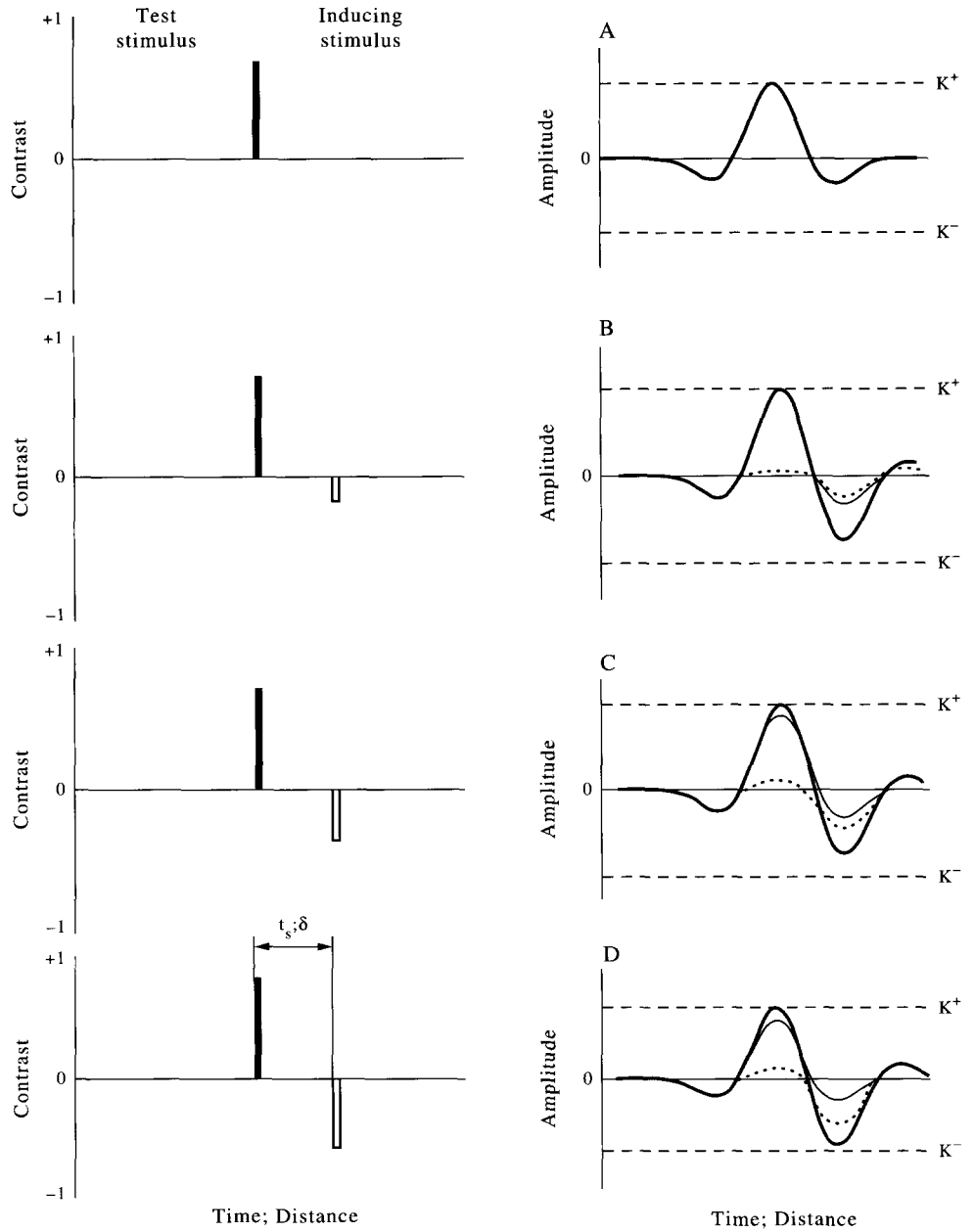

FIGURE 1. Left graphs show the inducing stimulus and the test stimulus at a given SOA (t_s) and a given distance (δ). (A) the ratio between the inducing-stimulus contrast and the test-stimulus contrast is zero; (B) −0.25; (C) −0.5; (D) −0.75. Right graphs represent imaginary responses to the test stimulus (thin lines), the inducing stimulus (dotted lines) and their sum (thick lines) at threshold level (K) for pattern detection of the test stimulus.

zero. If thus determined equation (3) is divided to C_tG_t (x_{extr}, 0, t_{extr}) then it could be written as:

$$C_0/C_t = 1 + (C_i/C_t)G_i(x_{extr} - \delta, 0, t_{extr} - t_s) / G_t(x_{extr}, 0, t_{extr}), \quad (4)$$

where C_0/C_t is the relative test sensitivity, C_i/C_t is the ratio between the contrasts of the inducing stimulus and the test stimulus at the pattern detection; and $G_i(x_{extr} - \delta, 0, t_{extr} - t_s)/G_t$ (x_{extr}, 0, t_{extr}) is the normalized amplitude of the impulse response to the inducing stimulus at a given moment and at a given distance along the x-axis.

The dependence of the relative test sensitivity and the C_i/C_t ratio is an equation of a straight line. Therefore, the slope of the linear regression line through the data points as a function of the SOA and the distance between the two stimuli may be considered a measure of the normalized amplitude of the visual response to the inducing stimulus in time and space.

METHODS

Apparatus

The stimuli were presented on a Tektronix 608 display with white phosphorus (P4) by electronics of our own design described elsewhere (Manahilov, 1995). The

frame rate was 200 Hz. The stimulus amplitude was controlled by a 12-bit digital-to-analogue converter.

Stimuli

The stimuli were vertical lines with duration of 10 msec. The screen with a mean luminance of 30 cd/m^2 was surrounded by a back-illuminated screen with almost the same luminance and hue. When the stimuli were presented foveally, the test and inducing stimuli were lines 1.4′ wide and 60′ long. Two black vertical lines (30′ long) continuously presented 30′ above and 30′ below the ends of the test line were used to direct the gaze of the subject to the test-stimulus position. In some experiments the stimuli were presented at 6 and 12 deg on the nasal horizontal visual-field meridian. In these cases the subjects fixated a small black spot. The size of the stimuli was extended in inverse proportion to the magnification factor which was calculated by the equation proposed by Rovamo and Virsu (1979). The lines subtended 4.1′ × 180′ at 6-deg eccentricity and 7′ × 300′ at 12-deg eccentricity. The stimulus contrast was calculated as $C = (L_{extr} - L)/L$, where L was the mean luminance and L_{extr} was the stimulus luminance.

Procedure

The staircase technique was used to measure the contrast threshold for pattern detection of the test stimulus. Two blocks of trials were used for every experimental condition: one consisted of an incremental test line and a decremental inducing line at four C_i/C_t ratios (0, −0.25, −0.50 and −0.75); in the other one, the polarity of both stimuli was changed, i.e., the test stimulus was a decremental line and the inducing stimulus was an incremental line at the same C_i/C_t ratios. With every block of trials, four staircases for pattern detection of the test stimulus in the presence of the inducing stimulus at the four C_i/C_t ratios were run simultaneously. Every trial began when the subject pressed a button and 500 msec later the stimuli were displayed. The test stimulus was accompanied by a tone. The subjects were instructed to report the presence of the test stimulus as a well-defined line of a given (positive or negative) polarity. They were required to press either the "seen the test stimulus" button at perception of a well-defined incremental (or decremental) line or the "not seen the test stimulus" button when a well-defined incremental (or decremental) line was not visible. The computer recorded the button press and automatically adjusted the contrast step size for the particular stimulus combination and staircase. If the current response was identical to the previous one for the stimulus combination and the staircase, the step size was kept unchanged. However, if the current response was opposite to the last one, then the step size was twice decreased. This process began at suprathreshold contrast levels with a contrast step of 0.2 log units and continued until the step size became 0.05 log units, remaining thereafter constant. Each subsequent staircase reversal was collected as a data point. In 20% of trials the test stimulus was presented with opposite polarity in order to check the subject's attention. The "false" responses were signaled by a tone. In all experiments only 2.5% "false" responses were registered.

Subjects

Four subjects took part in the experiments: the authors and two students, who were not acquainted with the purpose of this study. They had normal or corrected-to-normal visual acuity. The subjects viewed the stimulation field monocularly with the dominant eye (right eye) through the natural pupil.

RESULTS

The relative test sensitivity (expressed as a ratio between the threshold contrast for pattern detection of the test stimulus in the absence and in the presence of the inducing stimulus) as a function of the ratio between the inducing-stimulus contrast and the test-stimulus contrast is presented in Fig. 2. The data shown in the first and second columns of Fig. 2 were obtained with stimuli presented foveally on the same place at different SOAs. The circles and squares represent data about the pattern detection of incremental and decremental test stimuli, respectively. The graphs in the third column show data concerning stimuli presented simultaneously at different distances. The straight lines in Fig. 2 were obtained by fitting the data with equation (4) using the least square method.

Figure 2 shows that: (i) at SOAs of ±20 msec and a distance of 1.5′, the sign of the slope is positive; (ii) at SOAs of ±50 msec and a distance of 4.5′, the sign of the slope is negative; and (iii) at SOAs of ±120 msec and a distance of 10′, the sign of the slope is approx. zero.

Using the two-sample paired t-test, we established that the slopes of the calculated straight lines at pattern detection of the incremental and decremental test stimuli for every experimental condition and for all subjects were not significantly different at the 95% confidence level.

According to equation (4), the values of this slope may be considered a measure of the normalized amplitude of the visual response to the brief inducing stimulus at a given moment and at a given distance. The spatial spread of the line response was measured in the fovea and in the near periphery (6 and 12 deg on the nasal horizontal visual-field meridian). To this end, the lines were presented simultaneously at different distances between them. The mean values of the straight-line slopes were calculated by averaging the data obtained with incremental and decremental test stimuli collected in three or four experimental sessions.

Expressing the distance between the stimuli in units of the visual field (min of arc), the spatial spread of the line responses became broader with the eccentricity (Fig. 3). Only one half of the spatial spread of the line responses was measured, assuming that the responses were even functions.

To measure the impulse response in time, both lines were presented on the same site at different SOAs. The data of subjects RV and SA are illustrated in Fig. 4.

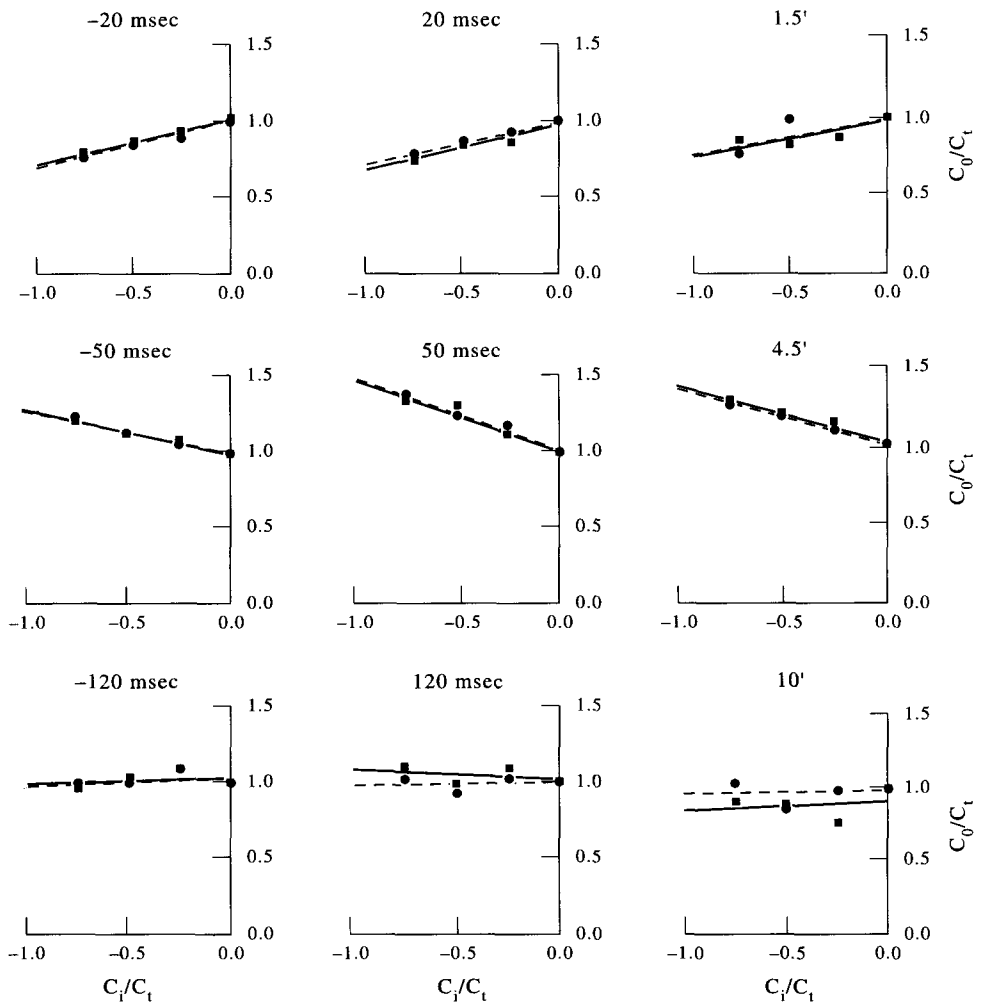

FIGURE 2. The relative test sensitivity (C_0/C_t) as a function of the C_i/C_t ratio between the inducing-stimulus contrast and the test-stimulus contrast. The relative test sensitivity is expressed as a ratio between the threshold contrast for pattern detection of the test stimulus in the absence and in the presence of the inducing stimulus. Circles: test stimulus is an incremental line; squares: test stimulus is a decremental line. First and second columns: both stimuli were presented on the same site at different SOAs as indicated by the number above each graph. Third column: both stimuli were presented simultaneously at different stimulus distances as shown by the number above each graph. Data of subject RV from one experimental session.

It is seen that the temporal-impulse responses are triphasic and their waveform is similar at foveal and peripheral stimulation.

The data about the temporal-impulse responses to foveal stimuli and 6- and 12-deg peripheral stimuli were assessed by the two-sample paired t-test for every SOA. It was established that the mean values did not differ significantly at 95% confidence level except for two data points of subject RV and subject SA.

At foveal stimulation, the line responses in space and time for every subject were fitted by equation (2). The least-square method was used to obtain the best-fitting values of the parameters (Table 1). Then, the data obtained on 6- and 12-deg peripheral stimulation were fitted by equation (2) with the relative magnification factor as a free parameter (Table 1).

It should be noted that for one of the subjects (SA) the value of the relative magnification factor at 12-deg stimulation differed from the values of the other three subjects. Since the data of the three subjects were similar, only the results of subjects SA and RV are presented here.

The lines in Figs 3 and 4 denote the model calculations with the values of the parameters shown in Table 1. In Fig. 4 only one line is illustrated because the calculated temporal-impulse responses to stimuli presented in the fovea and in the near periphery were similar. The goodness of the fit was evaluated by the analysis of variance (Manahilov, 1998—Appendix), which showed that the experimental data were adequately described by the model calculation at 95% confidence level.

DISCUSSION

In the present study, the responses in space and time to brief lines of near-threshold contrast levels were evaluated. To this end, the spatial spread and the temporal waveform of the responses were traced by a test stimulus which pattern-detection threshold was

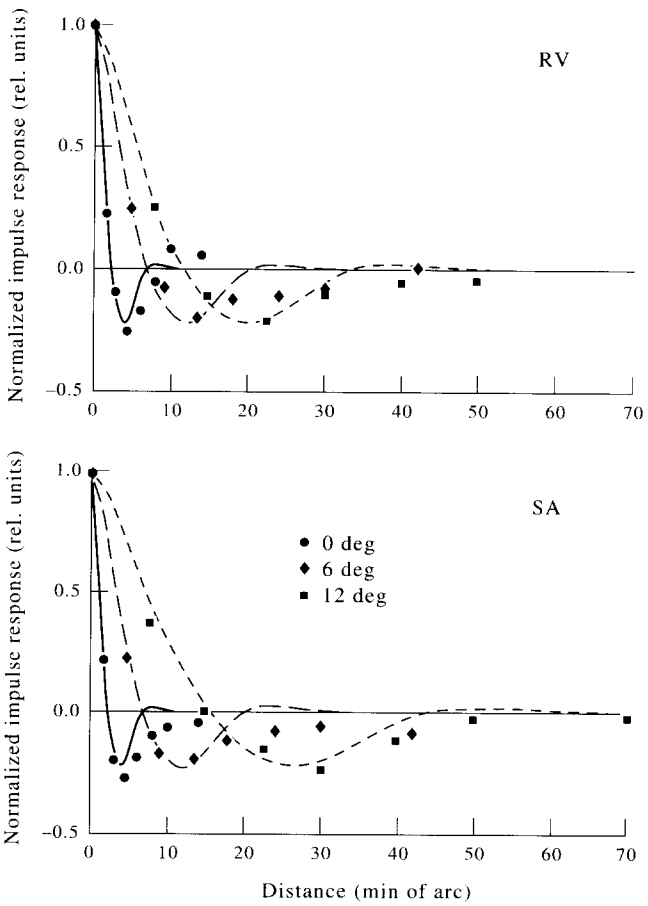

FIGURE 3. Spatial spread of the normalized impulse response in units of the visual field measured at stimulation of fovea (circles), 6 deg (diamonds) and 12 deg (squares) on the nasal horizontal visual-field meridian. Lines: spatial-impulse responses calculated by equation (2). Upper graph: data of subject RV; lower graph: data of subject SA.

assumed to depend on the peak of the test response. This approach is similar to the perturbation method proposed by Roufs and Blommaert (1981) and Blommaert and Roufs (1981) which is also based on the peak-detection assumption. However, these authors measured the threshold for contrast detection of impulse pairs. At contrast detection of stimulus pairs, the peak-detection assumption is not valid because every part of the response contributes to the stimulus detectability (Wilson, 1980; Watson, 1982). Owing to probability summation over space and time, the relationship between the threshold contrasts of the two stimuli was reported to be non-linear (Rashbass, 1970; Watson & Nachmias, 1977). At contrast-detection threshold levels, it is not possible to distinguish brief incremental stimuli from brief decremental stimuli and the stimulus contrast has to be increased above these levels to obtain a sensation of stimulus polarity (Rashbass, 1970). In the present experiments, when the test and inducing stimuli were of low contrast levels, they were perceived as a polarity-unspecified change in the screen mean luminance without seeing the test stimulus as a well-defined line. At higher contrast levels, when the test-stimulus polarity was identified, the test line was clearly visible. The test-stimulus polarity served as the cue used by subjects to distinguish the test stimulus from the inducing stimulus of opposite polarity. The threshold for pattern detection of the test stimulus was determined as the minimal contrast at which the stimulus was seen as a well-defined line of a given (positive or negative) polarity.

This pattern detection paradigm resembles the pattern

TABLE 1. Best-fitting values of the parameters obtained by fitting the experimental data from the four subjects with the model calculations by equation (2)

Parameters	RV	SA	VM	NJ
T (msec)	112	112	117	112
v (min arc/msec)	3.6	3.6	3.6	3.6
z (min arc)	20	20	20	20
τ (msec)	−15	−15	−24	−15
φ (msec)	7	5	9	10
σ	32	36	35	32
α	180	180	180	180
γ	160	165	156	156
m (0 deg)	50	50	50	50
m (6 deg)	16.6	16.6	16.6	16.6
m (12 deg)	10	7.7	10	

Parameters are explained in the Models section.

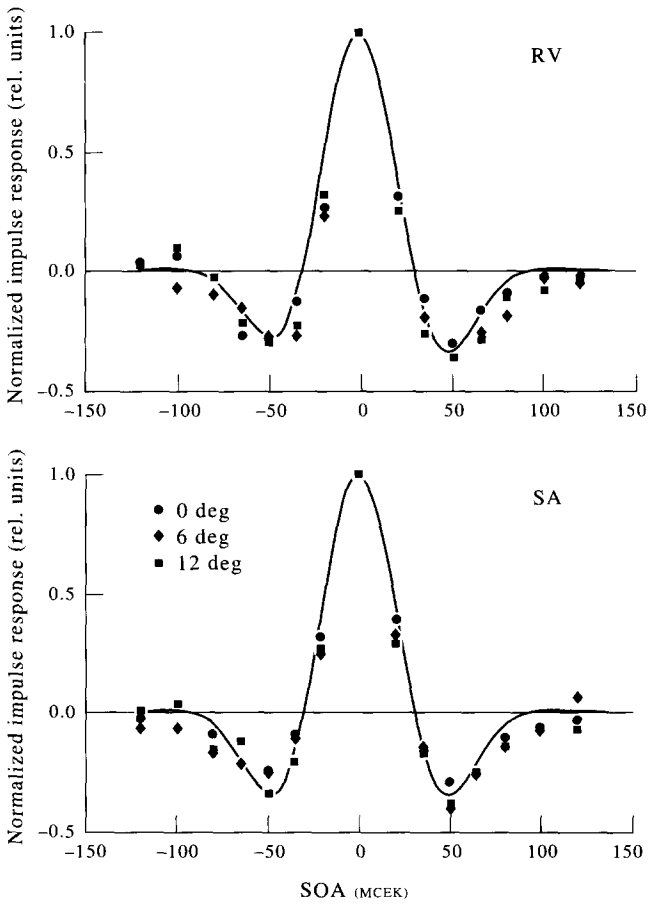

FIGURE 4. Temporal waveform of the normalized impulse response. The negative SOAs denote that the test stimulus precedes the inducing stimulus, and the positive SOAs that the test stimulus follows the inducing stimulus. Designations are as in Fig. 3.

detection of flickering line stimuli described by Keesey (1972). King-Smith and Kulikowski (1975) studied the contrast threshold for a flickering test line flanked by two subthreshold flickering lines. At flicker detection, they established the test threshold contrast depended non-linearly on the contrast of the flanked lines. However, at pattern detection, the relation between the test threshold contrast and the contrast of the flanked lines was linear. This finding corresponds to the linear dependence of the relative sensitivity to the test stimulus on the ratio of the inducing-stimulus contrast to the test-stimulus contrast (Fig. 2). This linear dependence supports the assumption that at pattern detection, the contrast threshold of the test stimulus is determined by the peak of the test-stimulus response.

It was found that the responses to line stimuli consist of positive and negative phases. Such responses could correspond to neural activity above and below an intermediate resting activity. However, the resting activity of most visual cells is too low to represent satisfactorily both directions of changes (Levick, 1973). At the bipolar cell level, two main pathways are created from the cones: the ON pathway consists of cells that discharge when their receptive-field center is stimulated by luminance increments and the OFF pathway consists of cells that are excited when luminance decrements stimulate the center of their receptive field. As a result of the center–surround antagonism, their responses are greatly attenuated when the stimulus is enlarged to include both the center and the surround of the receptive field. It has been suggested that the visual system evolved these parallel pathways to efficiently convey information about increments and decrements in luminance by excitatory signals (Jung, 1973). The ON and OFF pathways are thought to remain largely segregated in the primate geniculostriate system until they reach the striate cortex, where they converge upon single cells (Shiller, 1992).

The test and inducing stimuli of opposite polarity probably activate both ON and OFF pathways. However, one cannot determine with certainty the neural level of the visual cortex at which the responses to these stimuli interact. This is not crucial for the purposes of the present study, but the type of interactions (linear or non-linear) between the responses to the test and inducing stimuli is of importance. Recently, Bowen (1995, 1997) proposed a new approach to selectively activate cortical ON and OFF pathways and to study the ON–OFF pathway interactions. The author measured the masking effect of a large, long-duration, cosine grating on the contrast threshold for detection of a brief, spatially localized test stimulus defined by the sixth derivative of a gaussian (D6). Some of his data are closely related to the present results. When the test and masking stimuli were of opposite polarity and the SOA was 0 msec, the test threshold increased monotonically as a function of the masking contrast (Bowen, 1995). At masking stimuli of high contrast levels, the dependence of the test-threshold contrast on the masking contrast was described by a non-linear (power) function. However, at masking stimuli of low contrast levels, a linear dependence was observed implying linear interactions between pattern-specific cortical ON and OFF pathways. These linear interactions were described by a subtractive model which states that at near-threshold stimuli of opposite polarity, the residual detected test stimulus (the sum between the test threshold contrast and the masker contrast) is of a constant size and proportional to the unmasked test threshold. Therefore, the present results, as well as the Bowen data, conform to the assumption that the interactions between the responses to two near-threshold stimuli of opposite polarity are linear.

It is known that central vision differs from peripheral vision in many respects. Under photopic conditions, the processing of foveally and peripherally presented objects differs in the spatial scale at which the neural images are represented. When eccentricity increases, the density with which the cones sample the retinal images decreases, and the size of the receptive fields increases. On the other hand, the anatomical architecture of the visual cortex is quite uniform through the visual field, except for the decrease of the cortical magnification factor M [the linear extent (in millimeters) of the visual

striate cortex representing each linear degree of visual field] with the eccentricity (Daniel & Whitteridge, 1961; Hubel & Wiesel, 1974). According to the cortical magnification theory of peripheral vision (Virsu & Rovamo, 1979; Virsu, Nasanen & Osmoviita, 1987), the visibility of any stimulus is similar across the whole visual field if the stimulus size is proportional to M^{-1} (M scaling). The main purpose of M scaling is to equalize the number of retinal ganglion cells and postretinal cells stimulated at different eccentricities.

In some experiments, the magnification theory is tested indirectly by scaling the stimuli according to a prior estimate of M and afterward the performance is checked for its independence of the visual field location. Thus, observed deviations from the predictions of the magnification theory might be due either to a wrong magnification factor or to a failure of the theory.

Another approach (Wilson, 1970; Watson, 1987; Bijl, Koenderink & Kappers, 1992) has been used to test the magnification theory without prior knowledge of M. The contrast threshold is measured as a function of the spatial size of stimuli (disks, spatial Gabor patches, circular Gaussian blobs, etc.). If the magnification theory is valid then the contrast-threshold functions should be superimposed when shifted horizontally on log scale of the stimulus spatial parameter. The horizontal shift might be considered an estimate of the ratio of the magnification factors for the retinal locations tested.

It should be noted that both approaches for verifying the magnification theory are based on measurement of contrast detection thresholds. However, there are some factors affecting peripheral visual performance which are not related to the cortical magnification. The cortical effects of involuntary eye movements in central and peripheral vision are different. The peripheral refractive errors are an important factor for stimulus detection in the retinal periphery. Johnson and Leibowitz (1974) found that after the refractive errors were corrected the movement thresholds were lowered for all retinal locations tested, except for the fovea. The subject's practice had a little effect on the movement threshold in the fovea but much improved the movement detection in the retinal periphery.

In this study, the spatial spread and the temporal waveform of the response to brief lines were estimated at different retinal locations by a method which was based on measurement of the slope of the relative test sensitivity as a function of the C_i/C_t ratio. With this method, the cortical magnification theory could be verified without comparing contrast thresholds. This approach also provides direct information about the spatial spread of the line responses and the waveform of the temporal-impulse responses at foveal and peripheral stimulation. The stimuli presented in the near periphery were M scaled mainly because the available luminance range of the stimulation device was restricted. The exact M scaling was not crucial for the measurement of the line responses in space and time with the method described herein. Only the width of the line stimuli should be smaller as compared with the positive-phase width of the spatial line response.

The present results showed that at stimulation of the near periphery, the spatial spread (expressed in visual-field units) of the line responses became broader as compared with the spread in space of the responses to foveally presented stimuli (Fig. 3). This is in line with other psychophysical observations (Limb & Rubinshtein, 1977). The changes of the best-fitting values of the relative magnification factor with eccentricity were very close to the changes calculated by the expression of Rovamo and Virsu (1979). Only the data of subject SA at 12-deg stimulation were fitted by a value of the relative magnification factor, which was reduced by 30% more than the predicted reduction by the formula of Rovamo and Virsu (1979). This disagreement may be due to differences between the subjects. The expression for the magnification factor as a function of the retinal eccentricity (Rovamo & Virsu, 1979) might be considered an average evaluation of this relationship. The magnification factor in fovea has been reported to fall within the range of 6–15.1 mm/deg (Daniel & Whitteridge, 1961; Cowey & Rolls, 1974). The obtained value of 50 for the relative cortical magnification factor in fovea is in this range, because 1′ corresponds to 0.00485 mm, assuming that the posterior nodal distance of the human eye is 16.7 mm (Polyak, 1957).

According to the model of the spatiotemporal weighting function, the spatial spread of the line responses expressed in units of the visual cortex (mm) should not depend on the retinal site of stimulation. Figure 5 shows the data reploted from Fig. 4 by representing the distance in units of the cortical space. For every examined retinal eccentricity, the distance (in min of arc) between the test and inducing stimuli was multiplied by the value of the relative magnification factor according to Table 1 and a constant equal to 0.00485 mm/min of arc. It is seen that the line responses to stimuli presented in the fovea and in the near periphery are similar. The lines in Fig. 5 denote the calculated spatial-impulse responses to these stimuli at a cortical level by equation (2). Only one line is illustrated because the model responses to stimulation of different retinal locations coincided. For all subjects tested, there were no data points which differed from the model predictions by more than the 95% confidence interval.

These results support the suggestion of Virsu and Rovamo (1979) that image representations in space of the visual cortex are qualitatively similar for all retinal locations.

The model of the weighting function predicts that the temporal-impulse responses to line stimuli should be similar at foveal and peripheral stimulation. Indeed, under the present experimental conditions, the temporal course of the line responses remained unchanged (Fig. 4).

The data about this problem are rather contradictory. Virsu, Rovamo, Lairinen and Nasanen (1982) showed that the temporal frequency sensitivity functions to M-scaled stimuli presented in the fovea and the peripheral

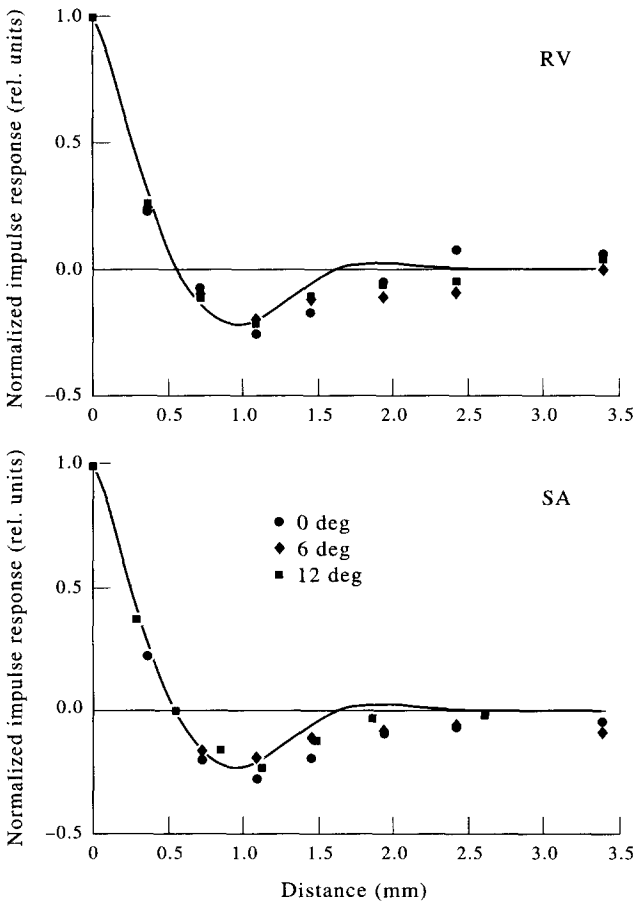

FIGURE 5. Spatial spread of the normalized impulse response in units of the visual cortex. Designations are as in Fig. 3.

retina were almost the same. On the other hand, Tyler (1985) reported that when the size of spots was *M* scaled, the peak of the temporal contrast sensitivity function remained approximately constant. However, the derived time constant (one half of the stimulus period at the peak sensitivity of the temporal contrast sensitivity function) decreased from a value of approx. 70 msec at foveal stimulation to approx. 45 and 38 msec at 6- and 12-deg stimulation, respectively. The author suggested that the time-constant decrease with eccentricity was related to the diameter increase of the outer segment of the peripheral cones. As Tyler (1985) noted, there is no physiological evidence to support this hypothesized relationship between receptor size and time constant. The assumption, that the form of the temporal contrast sensitivity function is determined linearly by the temporal impulse response of the visual system is valid in principle, but this function depends on the stimulus size which may not be *M* scaled exactly.

The waveform of the temporal-impulse responses to line stimuli of near-threshold contrasts consisted of three alternating phases, the middle one being the largest (Fig. 4). This finding indicates that the triphasic form of the temporal-impulse response is a common property of the visual system at both suprathreshold (Manahilov, 1995, 1998) and near-threshold stimulation.

To summarize generally:

1. The responses in space and time to a near-threshold inducing stimulus can be evaluated by the inducing-stimulus effect on the contrast threshold for pattern detection of a brief test line. With this approach, direct information about the spatial and temporal properties of the foveal and peripheral vision can be obtained.
2. The spatial spread in the cortical space and the temporal waveform of the responses to brief near-threshold lines were similar at stimulation of all retinal locations examined in the present study. These findings confirm the predictions of the model of the spatiotemporal weighting function. Therefore, this model can be used to predict the transformation of the retinal images in time and space of the visual network at stimulation of different retinal eccentricities.
3. The data obtained are in line with the cortical magnification theory of peripheral vision. The visibility of stimuli displayed at different retinal eccentricities might be similar if their size is *M* scaled because in the visual cortex the temporal-impulse and spatial-impulse responses are independent of the stimulated retinal site.

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